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A re-examination of Neomaruina (Diptera, Psychodidae), with observations on its life-history and affinities and redefinition of the tribe Psychodini

by

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ABSTRACT

New material of *Neomaruina* Vaillant, hitherto known only from the larva, allows the description of pupa and adult and a re-examination of the larva, including its mouthparts. The very *Maruina*-like larva appears to alternate between torrent dwelling and life as a member of the hygropetric fauna, and its adaptations to this habit are discussed. The pupa also is remarkably similar to that of *Maruina*, but the adults prove that *Neomaruina* is actually related to *Psychoda* Latreille and other genera of the Psychodinae–Psychodini. The Psychodini, *sensu* Quate, is shown to be based on a series of apomorphisms which firmly establish it as a separate phyletic line. *Neomaruina* is redefined, and the following species included therein: *stuckenbergi* Vaillant and *torosa* sp. n. from Zomba Mountain, Malaŵi; *deviata* (Tonnoir) **comb. n.** and *pseudomaxima* (Tonnoir) **comb. n.** from the Ruwenzori.

INTRODUCTION

Ventral suckers in stream-dwelling psychodid larvae were first noted in *Maruina* Müller (Müller 1895) from the neotropics, and later by Feuerborn (1932) and Tonnoir (1933) in the oriental *Neotelmatoscopus* Tonnoir and *Horaiella* Tonnoir. Subsequently, Vaillant (1963*a*) described an African larva with ventral suckers, regarded by him as a new genus and species, *Neomaruina stuckenbergi*, but the adults being unknown, the true affinities of this curious form were indeterminate.

The original material was collected in 1958 from Mandala Falls at 1 500 m on Zomba Mountain, Malaŵi, by Dr B. R. Stuckenberg, and in November 1980 he was able to return there, this time with Dr J. Londt, to seek more specimens. The outcome was a further larva, an incomplete pupal case, and 12 adults of two species that he thought also belonged to *Neomaruina*. In the present paper I find that this identification was correct.

Vaillant thought the Zomba larva was 'more closely related' to *Maruina* than to *Neotelmatoscopus* or *Horaiella*, but that it had certain 'very special features' which led him to place it in a separate genus. The very special features appear to have been the number and position of its lateral setae, and the number of ventral suckers, but as may be seen from his descriptions of two *Maruina* larvae (1963*b*), it is linked strongly to that genus by a large array of characters, predominantly apomorphisms. Its suckers are almost identical in structure, and the only features that, in retrospect, seem to hint at other affinities, are some pertaining to the antenna, siphon, and mouthparts, as described below, whose significance was overlooked. Thus, I disagree with Vaillant's (1983) view that immatures of *Maruina* (Tribe Maruinini) are 'perfectly distinct' from those of all other Psychodinae. Considered alone, the larva of *Neomaruina*, as also its pupa, is so similar to

Maruina that it would have been logical to regard it as an African *Maruina* which had diverged in isolation. Yet the apomorphisms of the newly discovered adults prove that it is indeed a separate genus, related, surprisingly, to *Psychoda* and other members of a quite different tribe, the Psychodini. The phylogenetic significance of this incongruence will be discussed in a later paper.

The occurrence of *Neomaruina* in East Africa

Zomba Mountain is a steep-sided and isolated plateau in the Chilwa Alkaline Province of southern Malaŵi, on the eastern side of the Shire Rift Valley. It appears to have been formed as one of a series of alkali granite and syenite intrusions, injected into the basement rocks in the Early Cretaceous and probably exposed progressively by erosion of the surrounding strata (Dixey 1956, Woolley & Garson 1970). Dr Stuckenberg says the mountain itself has a reliable rainfall and rich flora, including indigenous forest, but the surrounding areas are not montane, and are very hot. Jackson (1961) shows for Zomba a mean annual rainfall of 56 to more than 64 inches.

How two species of *Neomaruina* came to be on Zomba is a matter for speculation, but in view of its limited area (*c*. 9 × 21 kms) it seems unlikely that both evolved *in situ*. Two further species are known from the Ruwenzori, and since little specialised collecting of psychodids has so far been attempted on the other mountains of E. Africa, it is probable that this is a larger and more widespread

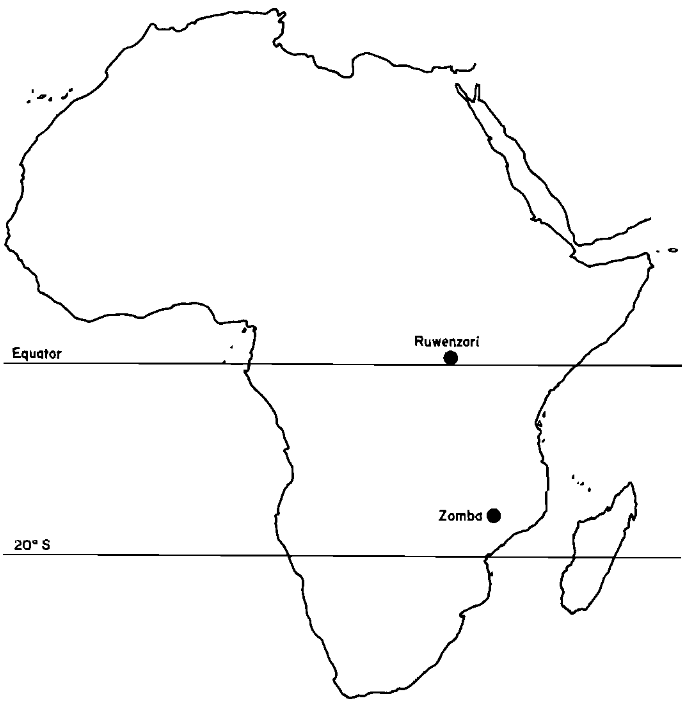


Fig. 1. Distribution of *Neomaruina*.

genus than is so far apparent. All species were collected at altitudes of 1 500–4 270 m, between latitutdes 0–15°S (Fig. 1).

Adults of *Neomaruina* resemble *Psychoda*—a genus with a strong capacity for dispersal, as shown by its common occurrence in the aerial plankton and by the existence of many apparent endemics on southern oceanic islands. It is therefore possible that *Neomaruina* reached Zomba by direct aerial dispersal from other E. African mountains, or less plausibly by spreading across the intervening country when the climate was wetter.

MATERIAL AND METHODS

Vaillant deposited two syntypes mounted on a single slide in the Natal Museum. From these I have selected as lectotype the larger of the two, which is also the one shown in dorsal view. This specimen is now ringed on Vaillant's slide. The new specimens will be placed in the Natal Museum with the types of *stuckenbergi*.

Immature stages were prepared using the method of Satchell (1949), then mounted whole in Canada Balsam. Most illustrations were drawn at this stage, but later the larva was dissolved from its slide and dissected, to obtain more details of mouthparts and suckers.

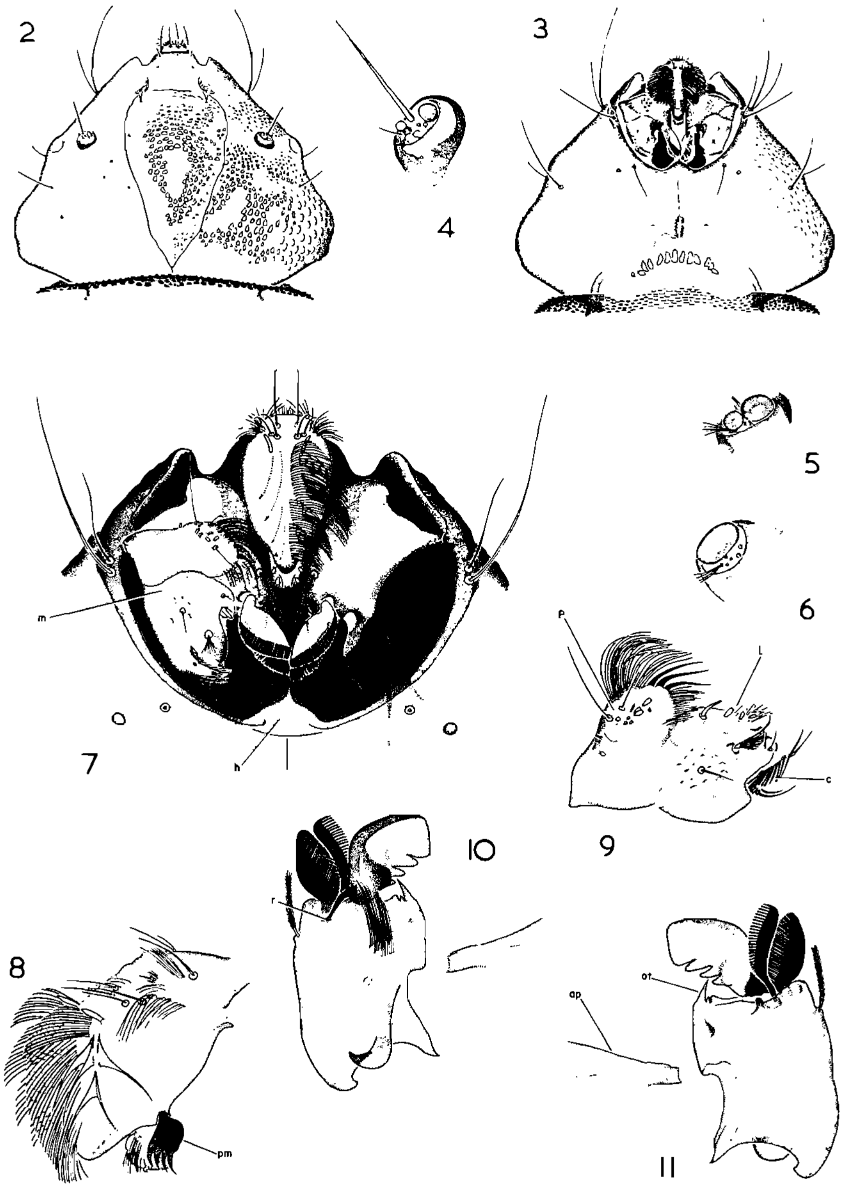
ANATOMY OF THE LARVA OF *NEOMARUINA*

The larva collected by Stuckenberg and Londt in 1980 agrees with the lectotype of *stuckenbergi* in all critical details, and is probably the same species. Nonetheless, I have not attached a species name because the two species of *Neomaruina* on Zomba have very similar adults, and their larvae may be virtually indistinguishable.

In this section I have re-examined the larval anatomy of *Neomaruina*, emphasising aspects neglected or inadequately dealt with in the original description, or which are of special adaptive or phylogenetic significance.

Head (Figs 2–3). Genae enlarged posterolaterally, giving roughly triangular shape in dorsal or ventral view. Eyes lateral and protruberant, sides of head consequently undulate. Epicranial sutures forming Y with well-developed posterior arm (coronal suture), absent in most psychodid larvae. Frontoclypeal apotome narrow, forming acute angle posteriorly. Ventral ecdysial line prominent, ending posteriorly in parallel undulate lines. Dorsal and lateral surfaces of head with brownish denticles, more protruberant laterally, low elsewhere. Dorsal setae small to minute, some mid-genal setae (Duckhouse 1962) absent, pre-frontals vestigial. Antennae (Fig. 4) more dorsal and posterior than in rheophobe larvae, almost level with eyes; consisting of 1 very long tapered shaft (probable rheoreceptor) flanked by 2 short mushroom-shaped elements, and 5 minute sensilla—a lateral seta and 4 sensory cones or domes. Thus, there are 8 antennal sensilla as Vaillant says, but he omitted the long shaft, present on both types, and did not observe the characteristic mushroom sensilla.

Mouthparts (Figs 7–11) sunk in small preoral cavity, rounded in outline, less than half length of head, bounded by subgenal edge. Hypostomium a small plate with 1 acuminate median tooth. Labrum (Fig. 8) a narrow, little sclerotised lobe with overlapping longitudinal rows of setae, some apparently with very broad, flattened



Figs 2–11. 2–4. Larva of *Neomaruina:* (2) dorsal and (3) ventral view of head; (4) antenna. 5. Larval antenna of *Threticus sp.* 6. Larval antenna of *Psychoda penicillata* Satchell. 7–11. Larva of *Neomaruina*: (7) mouthparts *in situ*, left-hand maxilla removed (*m*, right hand maxilla; *h*, hypostomium); (8) labrum and labrum epipharynx, lateral view (*pm* premandible); (9) right-hand maxilla, ventral view (*p*, palp; *l*, lacinia; *c* comb); (10) left hand mandible, inner side (*r*, retrobasal process); (11) left-hand mandible, outer side (*ot* opposed tooth; *ap*, tendon of adductor muscle).

bases, rapidly tapering into the shafts; premandibles with 4 long, pointed teeth; labrum epipharynx small, with fine setae and 4 sensilla, sensilla bulb-shaped in ventral view. Maxilla (Fig. 9) lightly sclerotised; palp proportionately larger than in most Psychodinae, with diverse small sensilla ventrally, and on medial surface a brush of long, fine, curved setae, and 3 stout broad-based setae; lacinia with sparse covering of sensilla, but no sclerotised teeth or domes as in most Psychodinae; posterior margin of maxilla with comb of setae (*c* in Fig.). Mandible (Figs 10–11) 2-segmented: proximal segment almost quadrangular, as in *Philosepedon* Eaton, *Trichopsychoda* Tonnoir and *Feuerborniella* Vaillant; strong ventral hook at base and acute opposed tooth distally, on inner margin; prostheca with 3 rows of bristles, longest reaching level of tip of opposed tooth; brush seta and 2 enlarged pectinate setae, one broad and leaf-shaped with comb of fine teeth, other narrow with coarse teeth, inserted above base of distal segment. Distal segment with 1 massive apical tooth preceded by 3 small teeth; shelf-like ventral element above bases of first 2 teeth; elongate retro-basal process (*r*) on ventral side.

Trunk somewhat flattened dorsoventrally. *Ventral surface of trunk* modified by development of complex mechanism for attachment to substrate, interpretable as single sucker subdivided by secondary partitions, or series of suckers partially united by fusion. There are 7 compartments, first larger than following 6, and as Vaillant recognised, derived from ventral surfaces of the 3 thoracic and first abdominal segments. The other 6 compartments correspond to 6 remaining presiphonal abdominal segments. Main fringes formed from regular palisade of long, stout, close-set integumental setae, flattened and with brush-tips; lateral fans, at anterior ends of main fringes, formed of setae with divided tips; transverse partitions of a line of far shorter and finer setae, apparently without brush-tips, backed by dense tomentum of long, fine integumental hairs arising from cuticular placques. Vaillant says transverse partitions each formed of a double row of anteriorly curved setae, which appear in his Figs 3a and 4a to be as stout as the elements forming the main fringes, although shorter and tapered to simple points. In the types they are far less stout than lateral elements, and backed by a tomentum of integumental hairs, as described above. Elsewhere within margins of suckers, placques more widely spaced but with similar elongate hairs peripherally, many times longer than shown by Vaillant, Fig. 4b. Placques outside suckers are simple domed structures.

Dorsal surface of trunk (Fig. 12) showing strongly reduced setae and loss of meso- and metathoracic mesotergites[1]. Setae placed as shown by Vaillant (Figs 2e, f) but mostly brush-shaped, not simple shafts. Dorsal surface of trunk with dense covering of sclerotised plates and placques, the smaller ones mostly mushroom- or stud-shaped (Fig. 13)—broad hollow base connected with flattened distal plate or knob by narrowed stalk region. Inter-annular placques (Fig. 14) with 1 or more

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[1] According to Feuerborn (1927), Jung (1956) and Satchell (1949), in typical Psychodidae - Psychodinae the mesotergites are missing from the thoracic segments, which therefore have two plates each (protergite and metatergite). However, in such forms the anterior tergite on each thoracic segment has true setae, while the abdominal protergites do not. This suggests that the remaining anterior thoracic plates are actually mesotergites and that it is the protergites that are lost. In *Neomaruina* the meso- and metathoracic mesotergites are also lost, leaving metatergites only on these segments.

pointed teeth or spines. Posterior abdominal segments curved strongly backwards laterally.

Siphon[1] (Figs 12, 15). Short and stout; apex broad relative to base. Dorsal surface (Fig. 12) sculptured with low dome-shaped papillae, and with 2 pairs of sensory setae, anteriors small and unbranched, posteriors larger and brush-shaped. Siphonal processes fringed with flexible, ciliated accessory setae, more than half as long as siphonal plate; ventral processes about 0,35 times length of siphonal plate, stout, annulated, horizontal, with setae forming horizontal fan; dorsal processes only about 0,24 times as long as ventral processes, without annulations, accessory setae forming almost vertical fan. Fringe of accessory setae behind posterior margin of siphonal plate (*terminal fringe* of Hogue, 1973) also ciliated and about half as long as siphon. Siphonal plate extended ventrally to fuse with lateral plates and entirely surround anal and adanal plates in a roughly circular anal foramen (Fig. 15). Anteriorly, 2 pairs of lateral setae in position occupied by lateral plates in many Psychodinae, and 1 pair of minute ventral siphonal setae on anterior margin, not shown by Vaillant, in line with setae of lateral plate but concealed by hinder edge of seventh abdominal segment. Vaillant (Fig. 2k) shows an additional lateral seta flanking foramen more posteriorly, but this is not present in his Fig. 4e, is not visible on the types, and is absent from the present larva. 4 anal papillae ('gills'). Preanal plate with 2 pairs of setae, as in all other Psychodinae; adanal plates with 4 setae on one side, 3 on the other.

Vaillant says the tergal plates have a complete set of true setae—as many as in the larva of *Telmatoscopus decipiens* Eaton (= *Paramormia decipiens*)—but mesotergite 1 has only 6 true setae, as compared with 7 in *decipiens*, although there is an additional seta, far lateral to the plate, which may be the one which is missing. The abdominal mesotergites also have only 2 true setae, compared with 3 in *decipiens*, but again there is another far beyond the plate, almost a lateral seta, and unless it belongs to the mesotergite it has no homologue in other Psychodidae. He also says that the anterior annuli of the second and third thoracic segments are 'entirely missing', but although the anterior tergal plates have been lost, the basic annulation of the thorax is as in other Psychodinae: the segments have two well-formed lobes on each side, and as he shows, the corresponding pleural setae are also present.

ADAPTATIONS OF THE LARVA

Neomaruina larvae show features, including ventral suckers, a streamlined body form, and well-developed siphonal processes fringed with long setae, that adapt them to life in streams under truly aquatic conditions. This does not mean that they would always, or even usually, be found submerged, but their survival is likely to depend upon an ability to live aquatically, for in all streams the water level and speed of current rise considerably at times, often rapidly, and small larvae on exposed rock surfaces may then be unable to retreat from the water. These are the

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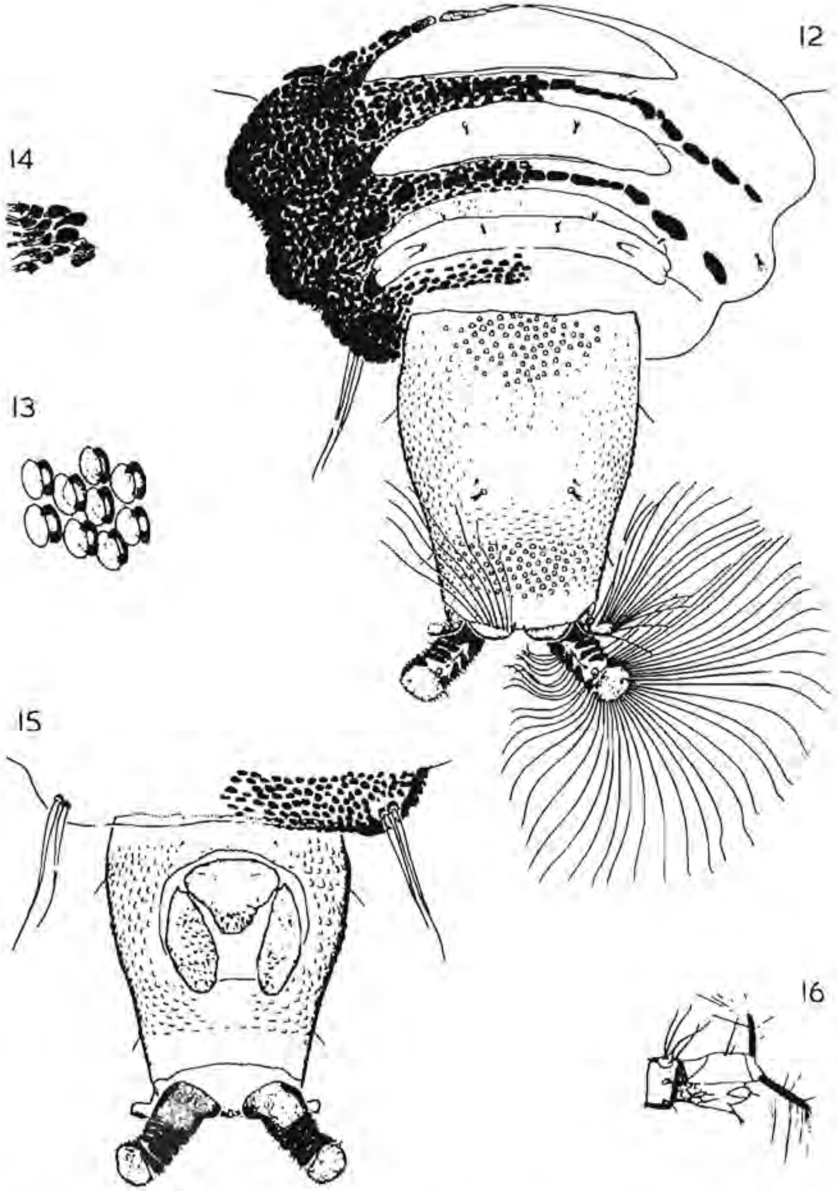
[1] Vaillant describes the siphon as 'abdominal segment VIII', but Satchell (1949) says the terminal region, beyond the seventh segment, 'is a compound structure derived from portions of segments 8, 9 and 10. . .'.



Figs 12–16. 12–15. Larva of *Neomaruina*: (12) seventh abdominal segment and siphon; (13) mushroom shaped cuticular placques; (14) interannular placques; (15) ventral view of siphon; 16. *Bazarella neglecta* Eaton, lateral view of siphon.

kinds of limiting conditions to which animals must be adapted, and as admirably shown by S. M. Manton (eg. 1956) in her work on diverse arthropods, it is often only by considering them in relation to such conditions that their structure becomes explicable: some of the most crucial adaptations are only occasionally employed.

The larvae of *Neomaruina* collected in April 1958 were 'found attached to a clean, smooth, vertical face of a large rock bounding the main flow of the stream' (Vaillant, p. 338). Dr Stuckenberg says they seemed to be clustered at the surface, in the zone where the water slopped and splashed. This was just below a pool at the foot of a waterfall, and in the open, though surrounded by a pine plantation. The present collection was made a few hundred metres away on another branch of the stream, bordered with indigenous forest, and mostly shaded. The larva was taken from a rock pulled out of the stream, an estimated 4–8 cms below the surface, on a face bounding the main flow. With it were a single pupa (see below), larvae of a ceratopogonid, *Atrichopogon* sp., and pupae of a minute trichopteran.

Most collecting in rocky streams having been done when water levels were relatively low, it would be understandable if a false idea had often been received about the conditions to which their inhabitants are especially adapted, but with *Neomaruina*, the first group of larvae was taken at a time of high water flow (mid-April 1958), and the new material before the rains had started, when the level was low (24–27.xi.1980). Thus, the conditions described might have been thought to represent almost the extremes to which the larvae are exposed, but I note that some *Maruina* species with almost identical adaptive features are capable of living on rocks well beneath the surface 'in swift to torrential waters' (Hogue 1973). Similarly, Zomba Mountain being subject to spectacular thunderstorms with heavy falls of rain, from time to time its *Neomaruina* larvae may be deeply submerged in swiftly flowing water.

The structure of the larva suggests versatility of behaviour, with alternation between torrent dwelling and life as a member of the hygropetric fauna. When submerged, *Neomaruina* would adhere to the rock surface by means of its suckers, but should still be able to move across it (see below), grazing on aufwuchs, and respiring by means of a bubble of air held between the fans of setae on its siphonal processes. This mode of respiration is also seen in stream-dwelling psychodids from submerged mosses and filamentous algae, eg. *Bazarella neglecta* (Eaton) (Miall & Walker 1895); unnamed larva (Müller 1888); *P. blandula* Eaton. When the stream subsides the same larva probably maintains itself in the film of water over half-submerged objects, much as in *Tonnoiriella pulchra* (Eaton), or species of Dixidae. It would now be in direct contact with the air, and it is notable that as in *pulchra* the ventral siphonal processes and their fans of setae are almost horizontal, while the dorsal processes are abnormally short in relation to them. However, in *pulchra* the setae on the dorsal processes also form horizontal fans, while in *Neomaruina* they are almost vertical. In most Psychodinae, including *neglecta* and other similar moss and alga dwelling species, the ventral processes are inclined diagonally downwards, the dorsal processes are almost vertical, and the fans on both are far from the horizontal (Fig. 16).

While *Neomaruina* is moving in a water film, the same reduction of the dorsal setae that helps to streamline it for torrent dwelling presumably also enables it to remain within the film, without breaking through the surface. So also do the horizontal siphonal processes. Such a larva might sometimes find itself on the borderline between marginal and terrestrial conditions, where the water film is very thin, but I envisage that the curious mushroom- or stud-shaped cuticular placques (Fig. 13) would then lead water by capillarity from the substrate towards the dorsal surface, and constantly renew it to compensate for evaporation. Similar placques occur on the dorsal surface in *pulchra* and at least some *Maruina* species, but in *pulchra* they are more narrowly separated and tend to overlap in places.

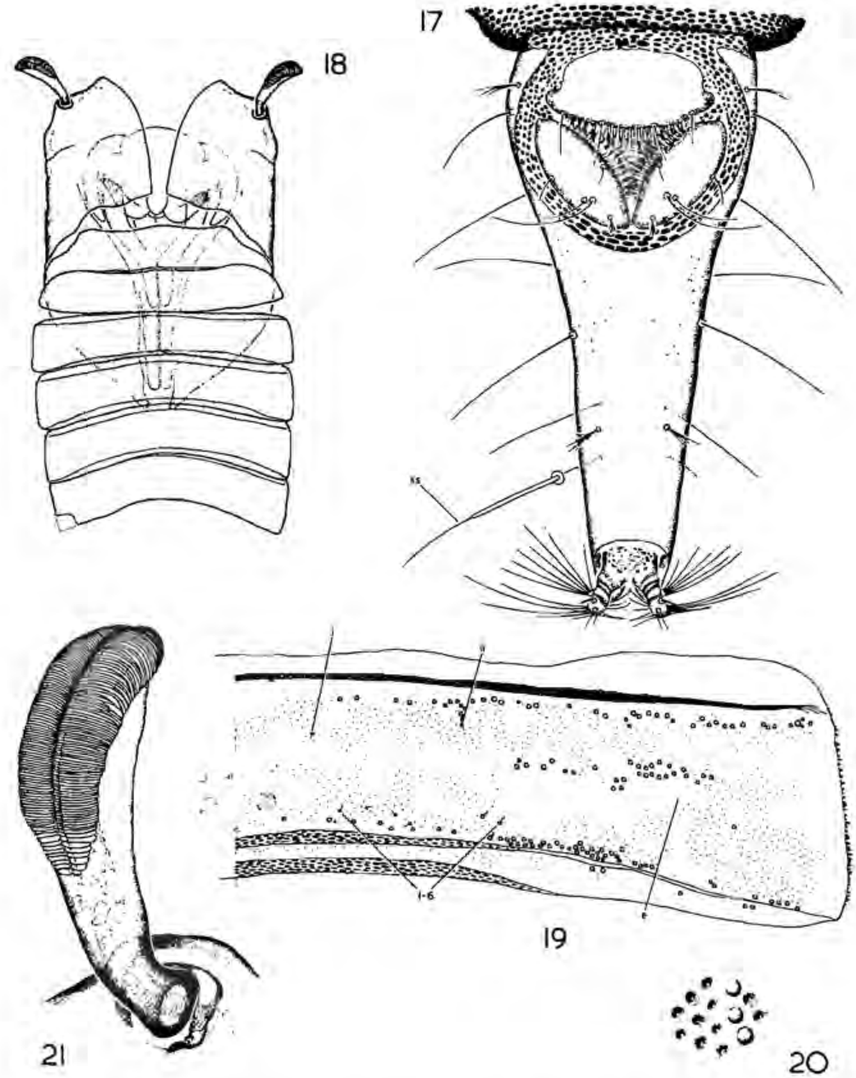
Vaillant (p. 339–40) says there is only one continuous sucker in *Neomaruina*, but the transverse partitions are well developed and I believe that the seven compartments may function separately. If they do, the larva should be able to move like a blephariceridby releasing only part of the sucking mechanism at a time, and thus to progress even when the current is strong. Subdivision of the sucker depends on the transverse lines of dense tomentum—essentially local concentrations in Vaillant's 'continuous coat of hairs' (p. 340). On such minutiae do organisms depend.

Tonnoir's (1933) theory of the evolution of ventral suckers envisages the initial development of one large sucker, as in *Horaiella*, which later became divided by transverse partitions to form a system conferring greater mobility, as in *Maruina* or *Neomaruina*. Finally, the compartments are rounded off to form fully separate suckers as in *Neotelmatoscopus*. Hora's (1933) objections to this theory do not seem to apply to psychodids, for the species with ventral suckers are not generally torrenticolous in Hora's more extreme sense. But although the sequence proposed by Tonnoir is plausible, *Maruina* and *Neomaruina* are not actually related to *Horaiella*, being in a separate subfamily, and thus there is no reason to maintain that these genera show secondary subdivision of the single sucker of an ancestral form. It is equally possible that rows of suckers present ancestrally became secondarily united in these lines.

THE PUPA OF *NEOMARUINA*

Included in the 1980 collection from Zomba is a single pupal case, lacking the tip and most of the ventral surface of the abdomen. Initially it seemed too large to correspond with the adults, but on closer examination I saw that it was merely broad and flattened, and that the sheaths of the adult structures were appropriate in size. Within the case I also found a teneral antenna, and several legs still enclosed in their sheaths, all showing the characteristic features of *Neomaruina* as described below. The venation visible on the wing sheaths is also of the type seen in *Neomaruina*. Since the case is split along its ecdysial lines it is probable that emergence was occurring at the time the collection was made.

Pupa (Figs 18–21) broad and dorsoventrally flattened; well sclerotised; 4th abdominal tergite (Fig. 19) with 8 minute sensory setae (*i, ii*; *1–6*) on each side, but no larger spines, setae or combs, etc., as seen in most members of this subfamily; dorsal abdominal cuticle (Fig. 20) with fine sculpturing of low papillae, especially prominent towards sides, and some darker, smoother areas *(e)* resembling the *escharae* of Hogue (1973); numerous conical sensory pits, each with central pore



Figs 17–21. 17. *Threticus sp.*, ventral view of siphon (*ss*, siphonal sensilla). 18–21. Pupa of *Neomaruina*: (18) dorsal view of whole specimen, back to sixth abdominal segment (remainder missing); (19) fourth tergite, right hand half (sensory setae, *i*, *ii*, *1–6*; *e*, escharae); (20) enlarged view of part of cuticle, fourth tergite, showing papillae and pits; (21) respiratory horn.

(?), appearing as punctuations on dark background; lateral margin of abdomen with small triangular teeth, giving fine serrate appearance. Those parts of ventral abdominal cuticle which remain bear papillae, but no sensory pits. thoracic region somewhat warty dorsolaterally.

Respiratory horns (Figs 19, 21) outwardly curved; felt chamber unbranched, coarse reticulate markings on inner wall as in some *Pericoma* species figured by Satchell (1949); 2 series of parallel elements (*rachi* of Hogue, 1973), derived from pits of more primitive species, arising from felt chamber in longitudinal groove on medial surface and curving outwards onto upper and lower surfaces of horn. Base of horn in thickened collar-like socket; enlarged at point of insertion but without annulations, and without the adjacent setae seen in most Psychodinae.

The pupa of *Neomaruina* is remarkably similar to that of *Maruina* as described by Hogue:–Dorsoventrally flattened, with a relatively smooth dorsal surface, and the median abdominal segments short and broad. The segments are also somewhat longer laterally than in the midline, and due to the cumulative effect of this the more posterior segments are curved backward at the sides, and the terminal segment, which is missing, would presumably be flanked on either side by the seventh.[1] The respiratory horns are displaced towards the midline, and their respiratory surfaces comprise two series of rachi as in Hogue's species *amadora, cholita, muchacha* and *doncella*, members of his more plesiomorphic subgenus *Aculcina*. *Neomaruina* also agrees with *Aculcina* in having the base of the horn enlarged, without annulations, and inserted in a stout collar-like socket. In species of the subgenus *Maruina* the base of the horn is generally annulated. The pupa of *Neomaruina* also resembles *Horaiella* in its respiratory horns, but Tonnoir (1933 : 58) claims, I think implausibly, that the anterior spiracles are actually open in *Horaiella*. There is no suggestion that this is so in *Neomaruina* or *Maruina*. Otherwise, especially in *H. prodigiosa* Tonnoir, the horn is strikingly similar, with the same deep fold or groove on one side and two series of rachi curving outward onto its sides. Again, the horn is enlarged at the base of the stalk and is not annulated.

It is probable that the *Neomaruina* pupa was attached to the substrate by the underside of the abdomen, and that this was left behind when the specimen was collected. Possibly it was firmly cemented, as in pupae of some other torrenticolous insects, for several sternites are actually torn, leaving small parts still attached to the corresponding tergites. Hogue (1973) says pupae of *Maruina* are 'bound to the substratum', while Vaillant (1963*b*) found that his species *boulderina* and *pennaki* were firmly attached like pupae of blephariceerids. *Horaiella*, too, is strongly attached, and Tonnoir says the adhesion seems to take place all round the edge of the body, but that the sticking fluid must also act on other parts of the underside, because detached pupae sometimes have tiny fragments of the friable rock still stuck to their ventral surfaces—on wings or leg-sheaths, but not at definite places. The far less modified pupa of *Neotelmatoscopus indicus* (Feuerborn) is cemented to the substrate by a mid-ventral 'Kittmasse' (Feuerborn 1932 : 65). The firm attachment to the substrate which occurs in these forms contrasts with the behaviour of other psychodids, many of which are stream-dwelling, but except for *Sycorax*, none are known to have attached pupae. Attachment is essentially an adaptation of psychodids whose larvae have ventral suckers.

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[1] The abdominal segments are similarly arranged in the flattened pupae of *Horaiella*, Blephariceridae and Deuterophlebiidae, and in larvae of Coleoptera–Psephenidae.

The fact that the pupa of *Neomaruina* was collected with the larva, about 4–8 cm below the water surface, at a time when adults were on the wing, suggests that as in *Maruina* (Hogue 1973) the adults may be able to emerge from such pupae.

THE ADULTS OF *NEOMARUINA*

The collection from Zomba contains two closely related species of the subfamily Psychodinae, Tribe Psychodini, *sensu* Quate, with features corresponding to those of the adult fragments enclosed within the above pupa and which Dr Stuckenberg took to be *Neomaruina*. He says 'the stream was low, and the flies were common on the rocks, gyrating rapidly on damp surfaces fringing the running water' (*personal communication*, 13.i.1981). My first reaction on seeing them was that although taken in the same broad habitat as *Neomaruina* larvae, these psychodines might be quite separate taxonomically. Later, however, I found that the larvae of *Neomaruina* also have some features typical of Psychodini (see below), and recognising that it is highly improbable that the very *Maruina*-like pupa corresponding to the adults is separate from the equally *Maruina*-like larvae in the same habitat, I conclude that all stages belong to *Neomaruina*, and that *Neomaruina* is a member of the Psychodini. The adults are closer to *Psychoda*, and to a lesser extent *Epacreton* Quate, than to any other genus. This relationship is supported by their Y-shaped ascoids and flattened labellum with terminal fringe of teeth. *Neomaruina* also agrees with *Psychoda* in the appearance of the living flies, which have uniform greyish vestiture and fold their wings over the abdomen in a tectiform position.

Psychoda is almost the last genus with which I would have associated the larvae of *Neomaruina*, but it is very large and few of the immatures have been examined. The Australian larvae that I know are like those of the Palaearctic, but Satchell's (1954) collection data indicates that some of his New Zealand species could be aquatic. Thus, *simplex* 'is common . . . on a wet rock surface where a small stream trickles over a shaded vertical rock wall along the Bullock track'. *Psychoda inaequalis* was also abundant in this habitat; while *pulchrima* and *formosa* were swept from herbage bordering a small waterfall in the Leith stream, and *tridens* was quite common amongst grass bordering the Ross and Leith streams—all in the Dunedin area. The adults of these species appear to be fairly typical *Psychoda*, quite unlike *Neomaruina*.

The antennae of *Neomaruina* larvae (Fig. 4) are basically as in Psychodini and different from those of other Psychodinae, which lack mushroom sensilla and have 2 or more digitate sensory rods. For comparative purposes I illustrate the larval antennae of *Threticus sp.* (Fig. 5), and also of *Psychoda penicillata* Satchell (Fig. 6), in which there is, as usual, one large mushroom sensillum. *Neomaruina* is also linked to Psychodini by the form of the siphon:—In one undescribed South Australian species of *Threticus* Eaton (Fig. 17), the preanal plate is short and forms a compact group with the adanal plates, and the siphonal plate has expanded along its ventral margins, fusing with the lateral plates and beginning to surround the anal area. If this process were to continue, the preanal and adanal plates would finally be confined within an anal foramen, as in *Neomaruina*. The siphonal plate has also extended to fuse with the lateral plates in the unrelated species *Telmatoscopus dendrophilus* Vaillant, *Paramormia longipennis* (Krek) and *Notiocharis dimorpha* Satchell.

Tribe Psychodini

The Psychodini, established by Quate (1959) and one of the most distinctive tribes in the Subfamily Psychodinae, is based on the following apomorphisms:

1. Antenna with flagellar segments flask-shaped, except for terminal three, which are primitively reduced, bead-like and without ascoids or well-developed verticils. (In further transformations, some terminal antennal segments may be secondarily lost or fused in various combinations, or the 14th and 15th segments may re-develop necks).

*2. Ascoids Y-shaped, or derived from this type by loss of one of the two anterior branches (*Threticus*), or development of a third (some *Psychoda* species).

3. Wing pointed and R_5 ending precisely at apex.

4. Sc short and thick.

5. Wings held folded in tectiform position (*Psychoda, Feuerborniella, Neomaruina*).

*6. Thorax with stigma (pore) anteriorly on mesopleuron.

7. Erect hair present on R_1 (*Psychoda, Threticus, Feuerborniella, Neomaruina*).

8. Ninth tergite of ♂ with single pseudospiracular opening.

*9. Labellum flattened, with terminal fringe of sensory rods ('teeth') (*Psychoda, Epacreton*, some *Threticus* species, *Neomaruina*).

*10. Larval antenna with two mushroom-shaped elements flanking sensory rod, or secondarily reduced from this condition (*Psychoda*).

Some larvae of *Threticus* have a pair of siphonal sensilla as in *Psychoda* (eg. *Threticus sp.*, Fig. 17, *ss*), an apomorphism apparently unique to these genera.

In most Psychodini the basal segment of the larval mandible is broad and almost quadrangular, and the distal segment deeply inset from its outer margin.

Of the apomorphisms listed above, 4–8 are here newly recognised. Except for the third and eighth, which occur sporadically in Telmatoscopini, all are absent from that tribe. The adults of *Neomaruina* are shown to be Psychodini by the presence of characters 1–9.

Taxa included in Psychodini: Psychoda, Feuerborniella, Neomaruina, Epacreton, Philosepedon, Trichopsychoda, Threticus.

Vaillant (1972:37, 46) transfers *Threticus, Philosepedon, Feuerborniella* and *Trichopsychoda* from the Psychodini into the Telmatoscopini, primarily, it seems, because their labella are bulbous rather than flattened as in *Psychoda*. Yet a flattened labellum, which is apomorphic, also occurs in *Threticus fissipes* Quate &

Quate and *T. nana* (Tonnoir), but in none of his other Telmatoscopini. Moreover, a bulbous labellum is plesiomorphic at the tribal level and therefore does not form a link with Telmatoscopini. Similarly, the presence of a preanal plate in larvae of *Threticus, Philosepedon, Feuerborniella* and *Trichopsychoda* does not link them with Telmatoscopini, which also have this structure, because at this level it is a plesiomorphic feature, secondarily lost in *Psychoda*.

Vaillant's (1971, 1972) separation of the above genera from *Psychoda* is partly based on his observation (1971 : 41) that in *Psychoda* the larval antenna consists of one or two elongate sensilla, but as shown by Satchell (1947), in this genus it comprises 'a small mushroom-shaped structure, around the base of which a ring of sensory processes is grouped'. The corresponding figure in Vaillant (1971, text-fig. 165), labelled as antenna of *Psychoda grisescens*, after G. H. Satchell, shows the *siphonal sensilla* of *Psychoda gemina* Eaton, reproduced from Satchell's Fig. 23. This may help explain his classification, because the elongate siphonal sensilla of *Psychoda* differ from the antennae of any known psychodid, whereas its antennae are obviously similar to those of *Threticus* and the other psychodines classified by him as Telmatoscopini.

Hennig (1972) considers that the Psychodini *sensu* Quate is very probably monophyletic, and notes that Vaillant provides no argument for rejecting Quate's concept, or in favour of his own. I find that the genera placed in this tribe by Quate share the features listed above, which are apomorphic at the tribal level, and with exceptions apparent from the list, almost omnipresent. Those which are asterisked are unique to the Psychodini. However, there are further psychodine genera, as yet undescribed, so this tribe is not truly monophyletic in Hennig's sense, but paraphyletic.

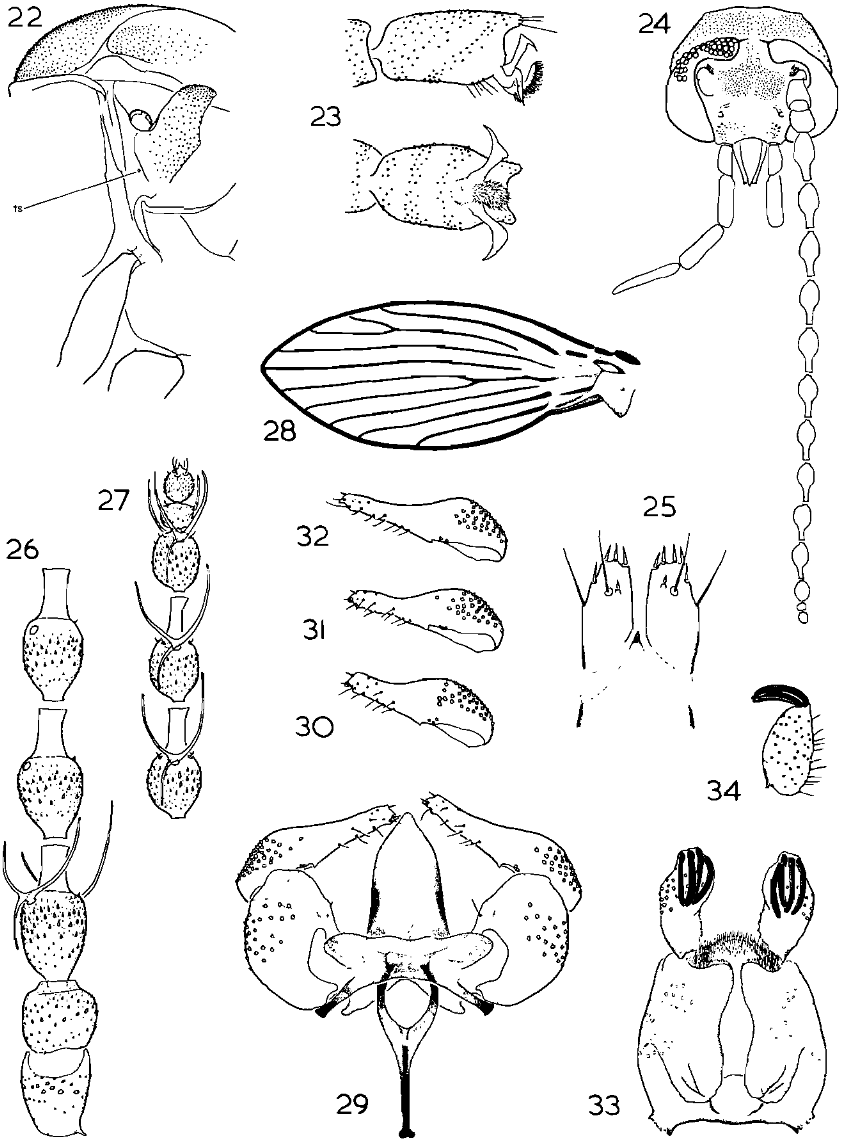
Genus *Neomaruina* Vaillant

Neomaruina Vaillant, 1963 : 338.
Type-species: *Neomaruina stuckenbergi* Vaillant, 1963 : 338, by monotypy.

Male and Female. Head broader than long; labellum short, flattened, with terminal fringe of sensory rods; palpi considerably longer than head, 1st segment about half as long as 2nd; eyebridges of 4 incomplete facet rows, constricted basally, distance between them usually greater than their width; scar patch on frons very wide, divided medially, posterior prolongation extending to between eyebridges. Clypeus scarcely extending beyond level of eyes. Antennae widely separated, 15-segmented (16th lost), 14th and 15th diminutive and ascoid-less, 15th inverted pear-shaped; ascoids Y-shaped, paired on segments 3–13; pedicel without dorso-medial dome-shaped organ of other Psychodidae.

Thorax with stigma (*ts*) anteriorly (Fig. 22). Wings folded in tectiform position. Wing without second costal node; pointed, R_5 ending at apex; Sc short and thick; R fork beyond medial and R_{2+3} more than twice length of R_2; erect hair on R_1. Legs with paired dorsal peg-like processes at tip of last tarsal segment (Fig. 23).

Male. Genitalia symmetrical; cercopods small and stocky, with several unstriated retinacula terminally; tergite 9 with single pseudospiracular opening and 2 lateral groups of hair scars; sternite 9 fused with aedeagal bridge.



Figs 22–34. Male of *Neomaruina stuckenbergi* Vaillant: (22) lateral view of thorax (*ts*, thoracic stigma); (23) last tarsal segment in lateral and ventral view; (24) head; (25) labellum; (26) base and (27) tip of antenna; (28) wing; (29) coxites, styles and aedeagus; (30)–(32) variation in structure of style; (33) ninth tergite and cercopods; (34) cercopod, lateral view.

Female. Subgenital plate short and broad; sensory organ above plate—probable homologue of genital digit of *Psychoda*—large, saccate, with scattered sensilla seen as pale areas on darker background. Cerci short, with peg-like tips.

There is no way of deciding with certainty which species on Zomba is *stuckenbergi*, but I tentatively take it to be the commoner of the two.

Neomaruina stuckenbergi Vaillant

Neomaruina stuckenbergi Vaillant, 1963 : 338, larva only.

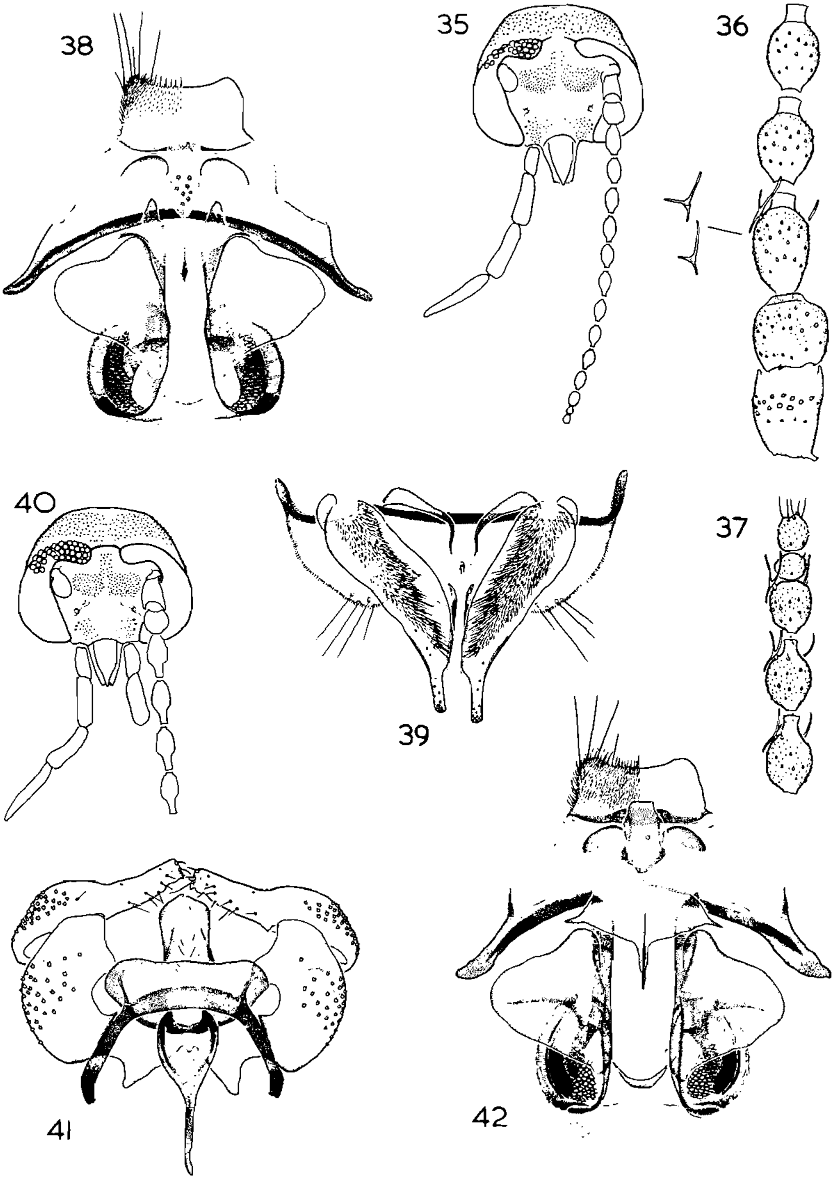
Small uniformly grey species; intromittent region of aedeagus large and shield-shaped, its sides rather regularly curved; cercopod with 4 retinacula.

Male. Head (Fig. 24) angular at base, 1,1–1,29 times as broad as long. Eyebridges separated by distance equal to about 1,2 times their width (about 5,2 facet diameters); connected by low arched interocular suture, unsclerotised in middle third. Scar patch on frons and its posterior prolongation completely divided along midline. Anterior tentorial tubes narrow, with large fan-shaped anteroventral flanges and small, rounded openings. Labellum (Fig. 25) slender; 4–5 tapered marginal rods on each side and one lateral seta; 1 short ventral rod and adjacent seta. Palpi, 1–1,75–1,9–2,3; stout, about 1,5 times length of head. Antennal insertion areas with oval sclerotised area on posterior margin. Antenna (Figs 26–27) stout, about 0,65 times length of wing; flagellar segments mostly with well-developed necks, about half as long as basal bulbs and delimited by crease; 13th segment with base narrower than apex, giving inverted pear appearance, 15th with apical tubercle bearing sensory seta. Ascoids extending beyond tips of segments bearing them.

Thorax, Fig. 22. Mesopleuron wing-like, apex curved over rim of notum. Wing, Fig. 28; R_{2+3} about 2,75 times length of R_2; membrane sclerotised, more darkly so in costal cell and above anal vein. Wing length 1,5–1,77 mm (8 specimens).

Genitalia (Figs 29–34) stout and compact. Forceps (Fig. 29) short; style somewhat longer than coxite, creased diagonally, distal half concave on outer side, apex broad, truncate, sensory setae as shown; coxite with two sensory setae ventrally on inner side. Variation in form of style, Figs 29–32. Intromittent region of aedeagus large, shield-shaped, sclerotised laterally and rather regularly curved to narrow apex; arising from transverse plate (aedeagal bridge) articulated dorsally with inner sides of coxites. Basal apodeme racket-shaped between bases of coxites, laterally flattened at apex. Central third of sternite 9 fused with transverse plate. Bases of coxites united beneath aedeagus by plate-like genocoxal apodeme, produced anteriorly into pair of short divergent lobes. Tergite 9 (Fig. 33) longer than broad; pseudospiracular opening large and circular; dorsal sclerite forming pair of plates, separated medially and fused with lateral margins of tergite. Tergite 10 a setose transverse plate with densely setose concavities at bases of cercopods. Cercopods (Fig. 34) only about half as long as tergite 9, each with transverse row of 4 claw-like retinacula.

Female. Head (Fig. 35) similar to ♂; less angular posteriorly, about 1,2 times as broad as long. Eyebridges narrower than in ♂, separated by distance equal to about



Figs 35–42. 35–39. Female of *Neomaruina stuckenbergi* Vaillant: (35) head; (36) base of antenna, inset showing ventral ascoids of first and second flagellar segments; (37) tip of antenna; (38) subgenital plate and spermathecae; (39) ninth tergite and cerci, ventral view. 40–42. *Neomaruina torosa* sp. n.: (40) male head; (41) coxites, styles and aedeagus; (42) subgenital plate and spermathecae.

1,4 times their width (5,8 facet diameters). Palpi, 1–1,7–1,9–2,4. Clypeus not extending beyond level of eyes, arched strongly backwards in midline above mouthparts. Scar patch on frons and posterior prolongation completely divided by median scar-free band. Antennae (Figs 36–37) 0,37 times length of wing; flagellar segments with necks only about a quarter as long as basal bulbs and delimited by crease. Ascoids small, some with unequal anterior arms.

Winglength 1,95 mm.

Genitalia, Figs 38–39. Distal lobes of subgenital plate (Fig. 38) short, almost parallel, microsetae sparse. Sensory organ inflated in appearance, without lateral wings. Spermathecae with radial striae laterally, cellular appearance medially. Apodemes including median structure with lateral wings immediately anterior to subgenital plate. Broad membranous sac anterior to spermathecae. Cerci (Fig. 39) 1,8 times as long as subgenital plate, which is itself short. Tergite 10 represented by pair of curved and tapered sclerites, articulated with cerci at bases, linked by membranous structure medially.

Material examined: 2 larvae (originally syntypes, now designated as *lectotype* and *paralectotype*), MALAŴI, Zomba Mountain (1535AD), Mandala Falls, 1 500 m, mid-April 1958 (Stuckenberg); 8 ♂ 2 ♀, same locality, montane forest, 24–27.xi.1980 (Stuckenberg & Londt).

Neomaruina torosa sp. n.

Intromittent region of aedeagus small with rather angular sides.

Male. Head (Fig. 40) rounded at base, 1,3 times as broad as long. Eyebridges separated by distance equal to about 1,5 times their width (5,4 facet diameters); connected by low arched interocular suture, sclerotised throughout. Scar patch on frons divided along midline, but posterior prolongation undivided, almost reaching interocular suture. Palpi, 1–1,5–1,6–2,1, about 1,5 times length of head. Base of antenna similar to ♂ *stuckenbergi*; ascoids and last 9 segments missing.

Winglength 1,93 mm.

Genitalia (Fig 41), similar to *stuckenbergi.* Forceps stouter; style robust with angular concavity on outer side and strongly truncate apex, sensory setae as in *stuckenbergi*; coxite with 2 sensory setae ventrally as in *stuckenbergi*, but concealed in figure beneath transverse plate of aedeagal complex. Intromittent region of aedeagus small, not shield-shaped; sides sclerotised, angular—expanding slightly then contracting abruptly just before apex. Transverse plate extending further posteriorly than in *stuckenbergi*; central third of sternite 9 fused incompletely with it, leaving distinct suture. Tergite 9 with pseudospiracular opening larger than in *stuckenbergi*, diameter more than one-third width of tergite. Cercopods about 0,8 times length of tergite 9, each with 5 retinacula, not arranged in single transverse row.

Female. Head about 1,2 times as broad as long. Eyebridges separated by distance equal to about 1,4 times their width (5,9 facet diameters); interocular suture unsclerotised medially. Palpi, 1–1,7–1,9–2,5. Scar patch on frons cleft anteriorly but otherwise undivided. Antennae 0,36 times length of wing, necks somewhat longer than in ♀ *stuckenbergi*.

Winglength 2,05 mm.

Genitalia, Fig. 42. Distal lobes of subgenital plate with microsetae denser than in *stuckenbergi*. Sensory organ with lateral wings anteriorly. Spermathecae larger and more widely separated than in *stuckenbergi*. Median apodeme with wings larger and with long median thickening. Membranous sac anterior to spermathecae more distinct than in *stuckenbergi* and its surface clearly pitted. Cerci 1,8 times as long as subgenital plate.

Material examined: Holotype ♂, MALAŴI, Zomba Mountain (1535AD), montane forest, Mandala Falls, 1 500 m, 24–27.xi.1980 (Stuckenberg & Londt). Paratype: 1 ♀ (allotype), with holotype.

Neomaruina deviata (Tonnoir) **comb. n.**

Psychoda deviata Tonnoir, 1939 : 46.

This species, collected at 1 675–2 290 m on the Bwamba Pass in the Ruwenzori Mountains, Uganda, is related to *stuckenbergi*. It differs in having completely black vestiture, cercopods about as long as ninth tergite and with numerous short, curved retinacula, and 13th antennal segment more distinctly pyriform than in the preceding species. Tonnoir says the labellum is 'very similar to that of *pseudomaxima*', but it has only 3–4 sensory rods in the distal fringe, compared with 7 in *pseudomaxima*.

Neomaruina pseudomaxima (Tonnoir) **comb. n.**

Psychoda pseudomaxima Tonnoir, 1939 : 44.

Collected from the Namwamba Valley at 3 045–4 270 m in the Ruwenzori Mountains. One of the largest known psychodids: winglength 3,9–4,3 mm, and thus at least as large as *Pericoma funebris* Hutton in New Zealand, though smaller than the New Guinean *Brunettia goliath* Quate & Quate, which has a winglength of 4,42–5,0 mm.

Known only from the female. Like the other species, *pseudomaxima* has a short ovipositor, in this instance scarcely longer than the subgenital plate, and the 13th antennal segment is pyriform. Labellum with distal fringe of 7 sensory rods, one ventral rod and 2 setae on each side. Eyebridges separated by distance equal to their width.

Adults of *Neomaruina* and *Maruina* agree in having short eyebridges connected by a low arched interocular suture, wide-set antennae, and a reduced ovipositor. Some *Maruina* species also have 15 antennal segments as in *Neomaruina*, but in most other respects adults of these genera are widely different and I believe the similarities may be independently derived adaptations to a similar habitat. The reduced ovipositor is possibly an adaptation to egg laying in rapid streams. It also occurs in *Neotelmatoscopus* Tonnoir.

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REFERENCES

DIXEY, F. 1956. Some aspects of the geomorphology of central and southern Africa. Alex. L. du Toit Memorial Lecture No. 4, *Geol. Soc. S. Afr., Annexure to vol. 52*: 1–58.

DUCKHOUSE, D. A. 1962. Some British Psychodidae (Diptera, Nematocera): descriptions of species and a discussion on the problem of species pairs. *Trans. R. ent. Soc. Lond.* **114**: 403–436.

FEUERBORN, H. J. 1927. Über Chaetotaxis und Typus der Larve und Puppe von *Psychoda*. (Zugleich 7. Beitrag zum Thoraxproblem). *Zool. Anz.* **70**: 167–184.

——— 1932. Die Psychodide *Maruina indica* sp. n. und ihre Beziehung zu den Blepharoceriden. Zugleich einige Mitteilungen über die Metamorphose von *Sycorax* und über Chitin als Klebemittel. *Arch. Hydrobiol. Plankt. Suppl.* **11**: 55–128.

HENNIG, W. 1972. Insektenfossilien aus der unteren Kreide. *Stuttgart. Beitr. Naturk.* **241**: 1–69.

HOGUE, C. L. 1973. A taxonomic review of the genus *Maruina* (Diptera: Psychodidae). *Natural History Museum, Los Angeles County, Science Bulletin* **17**: 1–69.

HORA, S. L. 1933. Remarks on Tonnoir's theory of the evolution of the ventral suckers of dipterous larvae. *Rec. Indian Mus.* **35**: 283–286.

JACKSON, G. 1961. *Map of climatic regions of Nyasaland*. Government Printer, Salisbury.

JUNG, H. F. 1956. Beiträge zur Biologie, Morphologie und Systematik der europäischen Psychodiden (Diptera). *Dt. ent. Z.* **3**: 97–257.

MANTON, S. M. 1956. The evolution of arthropodan locomotory mechanisms. Part 5. The structure, habits and evolution of the Pselaphognatha (Diplopoda). *J. Linn. Soc. Lond. (Zool.)* **43**: 153–187.

MIALL, L. C. & WALKER, N. 1895. The life-history of *Pericoma canescens* (Psychodidae). *Trans. ent. Soc. Lond. 1895*: 141–153.

MÜLLER, F. 1888. Larven von Mücken und Haarflüglern mit zweierlei abwechselnd thätigen Athemwerkzeugen. *Ent. Nachrichten* **14**: 273–277.

——— 1895. Contribution towards the history of a new form of larvae of Psychodidae (Diptera), from Brazil. *Trans. ent. Soc. Lond. 1895*: 479–483.

QUATE, L. 1959. Classification of the Psychodini (Psychodidae: Diptera). *Ann. ent. Soc. Am.* **52**: 444–451.

SATCHELL, G. H. 1947. The larvae of the British species of *Psychoda* (Diptera: Psychodidae). *Parasitology* **38**: 51–69.

——— 1949. The early stages of the British species of *Pericoma* Walker. (Diptera: Psychodidae). *Trans. R. ent. Soc. Lond.* **100**: 411–447.

TONNOIR, A. L. 1933. Descriptions of remarkable Indian Psychodidae and their early stages, with a theory of the evolution of the ventral suckers of dipterous larvae. *Rec. Indian Mus.* **35**: 53–75.

——— 1939. Psychodidae. *In*: *Ruwenzori Expedition 1934–5*. **1**: 35–80. British Museum (Natural History).

VAILLANT, F. 1957. Les larves de quelques espèces de *Telmatoscopus* et de *Pericoma* de la zone Paléarctique (Diptera Psychodidae). *Trav. Lab. Hydrob. Pisc. Grenoble* **49**: 71–108.

——— 1963*a*. An African psychodid larva with ventral suckers (Diptera: Psychodidae). *Ann. Natal Mus.* **15**: 333–343.

——— 1963*b*. Les *Maruina* d'Amérique du Nord (Dipt. Psychodidae). *Bull. Soc. ent. France* **68**: 71–91.

——— 1971, 1972. *In* Lindner, E. (ed.) *Die Fliegen der Palaearktischen Region*. 9d. Psychodidae – Psychodinae: 1–48; 79–108. Stuttgart.

——— 1983. Some Nearctic Psychodidae Psychodinae of the Tribe Telmatoscopini (Diptera). *Annls. Soc. ent. Fr. (N.S.)* **19**: 117–125.

WOOLLEY, A. R. & GARSON, M. S. 1970. *In* Clifford, T. M. and Gass, I. G. (eds.) *African magmatism and tectonics*. Oliver and Boyd, Edinburgh: 237–262.

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